

FOOD-RESOURCES AND THE INFLUENCE OF SPATIAL PATTERN
ON FEEDING IN THE PHORONID
PHORONOPSIS VIRIDIS

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The Phoronida are a coelomate phylum of vermiform, lophophorate tube-dwelling organisms. Although the phylum consists of but two genera and some eleven species (Emig, 1974), all resident in shallow marine waters (Hyman, 1959), it is possibly of great phylogenetic and ecological importance. Indeed, phoronids may well represent the most primitive of living deuterostomes (Zimmer, 1964) and the ancestral stock of the lophophorates (Valentine, 1973; Farmer, Valentine and Cowen, 1973). Ecologically, phoronids are often important in the structure of soft-sediment and fouling communities in that they may monopolize primary space (Ronan, 1975), a potentially limiting resource as in the rocky intertidal region. Despite the significance of the Phoronida, it remains a relatively obscure phylum which has not attracted the attention of many investigators. Hyman (1959) has reviewed the literature pertaining to phoronid biology. Work in English on the Phoronida has emphasized systematics (Marsden, 1959; Emig, 1974), developmental biology (Rattenbury, 1953; Zimmer, 1964, 1967), and genetics (Ayala, Valentine, Barr, and Zumwalt, 1974); phoronid ecology has received little attention (MacGinitie, 1935; Johnson, 1959; Ronan, 1975).

This paper examines the spatial pattern, feeding, and food-resources of the phoronid *Phoronopsis viridis*, a large phoronid with a pale green lophophore which inhabits intertidal localities in west coast embayments. In the past it has been assigned to *Phoronopsis viridis* (Hilton, 1930) based on specimens from Morro Bay, California, but it has also been synonymized with *P. harmeri* (Pixell, 1912) described from Vancouver Island, British Columbia (Marsden, 1959). Zimmer (University of Southern California, personal communication) believes the Canadian and Californian populations are specifically distinct, with the California form to be called *P. viridis*; I shall employ this name, although there is no work on geographic variation and relationships are uncertain.

MATERIALS AND METHODS

Study site

The study was conducted in Bodega Harbor, California (38° 19' N, 123° 03' W), a small marine coastal embayment located 100 kilometers north of San Francisco, California. The harbor is quite shallow (maximum depth, 4.0 m at low water). At mean lower low water (MLLW = 0.0 ft) extensive tidal flats, which occupy about 60% of the harbor, are exposed. The harbor is a depositional environment. Without periodic maintenance dredging, the harbor would revert to a lagoon.

Within the harbor there is a 0.5 mile² sand flat which is posted and maintained as a marine life refuge by the University of California Bodega Marine Laboratory. Phoronid and sediment collections were taken within the refuge and just to the north of the refuge. Feeding observations and nearest-neighbor (N-N) measurements were made within the refuge boundaries.

Field census and nearest-neighbor relations

The intertidal distribution and abundance of *Phoronopsis* were determined by hand excavation of square meter holes along two transects. The transects were roughly parallel to each other from MLLW to the mean higher high water (MHHW) mark (120 cm above MLLW). The distance between transect stations was 10 meters; the longer transect A had twice as many stations as transect B. Care was taken to establish the transect stations in areas known to be free from clam digging which can greatly modify the spatial pattern of *Phoronopsis*. During excavation, all phoronid tubes were separated from the sedimentary matrix and their numbers recorded. Phoronid numbers were estimated at 95% of the counted numbers of tubes because about 5% of the tubes in dense aggregations are known to be vacant (Ronan, 1975).

Nearest-neighbor measurements were made along transect A, at stations 3, 5, and 7, following methods proposed by Clark and Evans (1954). Spacing measurements were not possible at station 1 because phoronid tube apertures were occluded by flocculent seston which thickly mantled the depositional interface. Higher in the intertidal, the spatial pattern of *Phoronopsis* was easier to determine since the small holes produced by the animal at the sediment-water interface (SWI) remain open at low water. Because individuals of this species aggregate in clusters of up to thousands per m² throughout the study area, all N-N measurements are within cluster distances. At each sampling station, three 25 cm² frames fitted with clear plastic inserts were randomly dropped and the area occupied by the largest cluster circumscribed with a rectangle. Within the rectangle, the position of each animal was recorded on the plastic with a felt tip marker. Since only inhabited tubes had open apertures, cluster population density was accurately determined by counting the dots on the plastic. For all animals, distance to N-N was estimated as the distance to the nearest mm between the centers of the dots.

Feeding observations

Low intertidal sites (2 m²), each estimated to contain more than 17,000 *Phoronopsis*, were selected for detailed underwater feeding observations. The study sites were adjacent to transect A and separated from each other by 5 m. About six hours were spent underwater on various occasions observing phoronid feeding behavior.

As a phoronid lophophore is small and held close to the SWI, it is best to view it from the side. Feeding observations were made by SCUBA diving with a heavy weight belt and tethering to a short line anchored in the sediment nearby. Height measurements were made on nine clustered phoronids every 15 minutes over a 60-minute period.

Food resources

Early observations indicated that a feeding animal positions its lophophore within the turbid near-bottom layer of water (Ronan, 1975). The location of the feeding appendage is reflected in the animal's stomach contents in that the ingested materials primarily represent items resuspended from the SWI. To confirm this impression, food selection in relationship to the animal's available food was quantified by examining the food-resources of the SWI and the water column.

A large diameter (5 mm) pipette was used to collect seston (skeletal material, mineral grains, and organic particles) from the SWI around the tubes. The seston was preserved in 90% alcohol and examined under a dissecting microscope. Using the criteria of Johnson (1974), seston material was classified by particle type. Mineral grains were categorized by size and the presence or absence of encrusting organic matter. Loose aggregates of fine-grained minerals bound in an organic matrix were termed floc (organic-mineral) aggregates. Firm organic-mineral aggregates in the form of pellets, or fragments, were classified as either *Phoronopsis* feces (which are distinctive) or other fecal matter. The remaining material was listed as either plant fragments, pollen, diatoms, or small metazoans (copepods, nematodes, ostracods, etc.). Mineral grains were measured with an ocular micrometer. Particle type abundance categories (Johnson, 1974) were used to express the abundance of different fractions of the food-resources available to the organism.

During the same period (Sept.-Oct., 1975) in which phoronids were collected for stomach content analysis, plankton was also collected by towing a 0.25 m plankton net with 0.333 mm mesh size twice through the water with the base of the net no more than 10 cm above the bottom for two 15-minute periods. The entire sample was analyzed and particle type abundance categories (which were calculated by averaging the two samples) were used to express the relative abundance of the plankton species available to *Phoronopsis*.

Stomach contents

Twenty specimens of *Phoronopsis* were removed from their tubes, preserved in 90% alcohol, and the ingested material collected from the stomach. After the stomach fractions were washed in distilled water to remove adhering mucus, they were examined under magnification. The methods described above for analyzing particle fractions were employed to determine abundance of particle types and size distributions for the stomach samples.

The results of the analysis of abundance of different particle types are expressed as percentage of particle abundance. Whitlatch (1974) suggests the use of this measure in determining food selection because it reflects the relative amounts of different particles available in the environment of an organism.

Electivity coefficients of different particle types selected by *Phoronopsis* were determined using the statistic of Ivlev (1961). The statistic is calculated as $E' = (r_i - p_i) / (r_i + p_i)$. For the i th food type, r_i equals the percentage ingested and p_i is the percentage of that food type available in the environment. The coefficient is bounded and symmetrically distributed about zero ($E' = 0$ indicates

nonselective feeding; $-1 \leq E' < 0$ indicates avoidance; and $0 < E' \leq 1$ indicates feeding preference).

Phoronid fecal pellets were collected from the field with a small-diameter (2 mm) pipette, washed and disaggregated in sea water on a 250 μm sieve, and the contents examined under magnification. Particle size analyses of disaggregated feces were performed in distilled water.

RESULTS

Abundance and spatial distribution

Figure 1 shows the number of *Phoronopsis* excavated from meter-square quadrats along the two transects. In the intertidal zone, phoronids are aggregated in discrete clusters that are separated from other clusters by intervening open

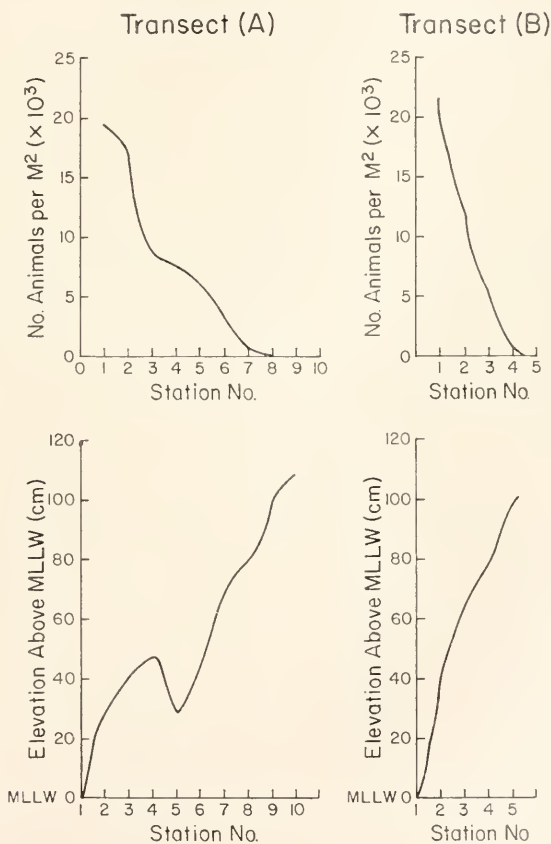


FIGURE 1. A and B (above) show the number of *Phoronopsis viridis* removed from square-meter excavations along two parallel intertidal transects; and (below) station elevations with respect to distance above mean lower low water. The sampling interval between stations was 10 m.

spaces where density is low. The clusters were largest and the densities greatest within firm sediments with a median particle diameter less than 250 μm . Along the transects which traversed fine sediment only, cluster density ranged from 21,422 phoronids/ m^2 at MLLW to zero at the highest intertidal stations; their upper limit roughly corresponded to the mean lower high water (MLHW = 100 cm above MLLW) line. The mosaic of irregular clusters and intervening open spaces was most obvious near the animals' upper limit where clusters were small (range: 3–67 phoronids) and their boundaries distinct. The most dense and continuous clusters were around MLLW, where aggregate clusters containing up to 150,000 phoronids and covering up to 10 m^2 occurred.

Phoronids were not distributed evenly throughout the low and mid-intertidal, however. *Phoronopsis viridis* was absent or rare in lenses of loosely packed sediment with a median particle diameter greater than 250 μm . In an elliptical bed of coarse sand (5×30 m) along transect A, located eight meters shoreward from the low tide line, cluster density declined from 12,116 phoronids/ m^2 at the periphery of the bed to 0/ m^2 , 1.5 meters into the interior of the coarse substrate. A smaller lens-shaped (5×8 m) body of coarse sediment occurred in the mid-intertidal. In this substrate, the cluster density of phoronids was very low, ranging from 9370 animals/ m^2 at the periphery to 0 animals/ m^2 at a distance of 0.5 m into the interior. Although the number of animals per square meter always declined in loose coarse sediment, the phoronids remain aggregated in small, tight clusters.

Table I shows the N-N frequency distribution for 2616 *Phoronopsis* in nine intertidal clusters composed of from 75 to 481 individuals. All of the measurements were made in fine sediment prior to the excavation of stations 3, 5, and 7 along transect A. The mean distance to N-N was 5.4 ± 2.8 (s.d.) mm with a range of 1–25 mm. The mode is slightly less than the mean, and the distribution has a long tail of distances greater than the mean.

N-N analysis of the dispersion pattern of *Phoronopsis* indicates the distribution

TABLE I

Frequency distribution of distances between individuals for 2616 *Phoronopsis viridis* in nine intertidal aggregations.

Distance (to nearest mm)	Frequency	Per cent	Cumulative percentage
1	92	3.52	—
2	183	7.00	10.52
3	401	15.33	25.85
4	516	19.72	45.57
5	360	13.76	59.33
6	341	13.04	72.37
7	293	11.20	83.57
8	125	4.78	88.35
9	136	5.20	93.55
10	33	1.26	94.81
11–13	79	3.01	97.82
14–16	36	1.37	99.19
>17	21	0.80	99.99

of individuals within clusters departed significantly from randomness. A mean R (\bar{R}) value for 9 clusters (cluster size 75–481 individuals; $N = 2616$) of 0.64 indicates that N-N were only slightly more than half as far apart as expected under conditions of randomness ($P < 0.01$). The mean N-N distance of 5.4 mm was roughly half the space required to expand two adjacent lophophores completely, without their impinging each other. Individuals crowded together in this manner were observed to stratify their lophophores vertically by some individuals extending their trunk above the SWI. Because the body wall is flexible, a phoronid can spread the lophophore away from neighbors by bending the extended trunk. Small N-N distances often produced an array of “tall” and “short-standing” phoronids as the individuals in a cluster maneuver for space to expand their lophophores. However, few ($< 11\%$) individuals of *Phoronopsis* were packed within 3 mm of each other. At such close distances, even a stratification of feeding appendages failed to provide for full expansion of adjacent lophophores; the N-N distances were so slight that an expanded lophophore would abut against the trunk of a neighboring “tall-standing” individual. Therefore, the distance from the lophophore of one individual to the trunk of an adjacent individual provides a measure of the lower limit below which feeding space cannot be reduced by a stratification of lophophores.

The lophophore

The action of the lophophore was observed microscopically in laboratory-maintained *Phoronopsis*. Currents produced by cilia on the tentacles bring water and suspended particles down within the loop of the lophophore and then out between the tentacles. The mechanics of particle capture, rejection, and food transport were found to be as described for *Phoronis vanconverensis* by Strathmann (1973).

There was no diel periodicity in feeding; animals fed continuously during tidal submergence. This observation was expected, since variations in food availability are not to be expected. Although the lophophore is perpetually bombarded by small particles cascading along the SWI, the animal is sensitive to disturbance and has a well-developed escape response. Contact between the tentacles of the lophophore and large tumbling fecal pellets and detritus produced a partial folding of the lophophore and retraction of the trunk. Predatory strikes at the feeding appendage by the nudibranch *Hermisenda crassicornis* resulted in a rapid folding of the lophophore and retraction into the tube. Only rarely was a large lophophore completely cropped by *Hermisenda*; most strikes removed only a few tentacles from the lophophore. However, a small phoronid can lose its entire lophophore to *Hermisenda* as well as to fishes which can remove even a large phoronid from its tube (Ronan, in preparation).

Feeding in clusters

Clustered phoronids were observed to sporadically vary the height of their expanded lophophores. The structure of the stratification undergoes continuous modification as the animals raise, lower, and interfinger their feeding appendages (Table II).

TABLE II

Sequential underwater measurements of the height of Phoronopsis viridis above the sediment-water interface.

Phoronid no.	Time (min)					
	0	15	30	45	60	\bar{x}
1	15	0	8	13	17	11
2	24	24	20	22	25	23
3	18	23	12	0	9	12
4	19	21	6	0	14	12
5	14	8	8	5	9	9
6	22	22	16	8	3	14
7	9	0	11	14	9	9
8	17	17	24	19	19	19
9	24	20	25	16	0	17
Mean height* of cluster	18	15	14	11	12	

* Height measurements were made by inserting a transparent metric ruler directly in front of the animal and recording the distance from the sediment-water interface to the base of the lophophore. The mean distance to nearest-neighbor was 4.9 mm with a range of 2–13 mm.

The longest trunk extension noted was 25 mm with the lophophore extending another 6 mm above the trunk. The trunk is flexible so that an animal may bend away from and expand the feeding appendage above surface obstructions. Periodic height adjustments maintain the stratification and safeguard against impingement between neighboring lophophores.

Seston composition

Analysis of the food-resources of the SWI revealed that three particle types averaged over 69% of the potential available food: small ($< 100 \mu\text{m}$) encrusted mineral grains, floc aggregates, and *Phoronopsis* fecal pellets (Table III). Small encrusted mineral grains were usually the most abundant particle type. The encrusting material varied in its consistency and degree of adherence. When the organic matter attached to mineral grains is stained with the periodic acid-Schiff (PAS) histological reagent, it characteristically gives a strong positive reaction, thus suggesting the encrusting material is largely carbohydrate (Johnson, 1974; Whitlatch, 1974). Small encrusted mineral grains plus floc aggregates, the second most abundant particle type, together averaged more than 56% of the available particulate material.

Floc (organic-mineral) aggregates comprised the second most abundant particle type in the samples examined. Floc material consists of very fine-grained mineral matter, incorporated into an amorphous organic matrix (Johnson, 1974; Whitlatch, 1974). Not all floc material is the same. Some aggregates were rich in mineral matter, tightly bound by the matrix material. Other floc material consisted of a loose indistinct matrix with few bound particulates. From extensive staining experience, Johnson (1974) and Whitlatch (1974) conclude that

the matrix of organic-mineral aggregates is largely carbohydrate. Floc material was always abundant in harbor water samples collected from just above the SWI and was especially abundant in samples collected from the low intertidal zone and tidal channels. Rhoads (1973) has reported that different types of floc material may differ in floc bulk density and ease of resuspension.

Fragmented fecal pellets of *Phoronopsis* were the third major particle type. Intact pellets are spindle-shaped rods up to 7 mm in length, which are rich in silt and clay. Natural decomposition of the mucous envelope which binds a pellet produces many stringy fecal fragments. There was a strong morphological resemblance between naturally decomposing phoronid fecal matter and the floc material complexed with mineral grains (organic-mineral aggregates).

All three common categories of seston (small encrusted mineral grains, floc aggregates, and fecal pellets) were resuspended by tidal currents and wind-driven waves. Hence they were readily available to *Phoronopsis*. The remaining particulate material consists of large mineral grains ($> 100\ \mu\text{m}$), plant detritus (fragments of *Ulva expansa* and *Zostera marina*), living diatoms, pollen, and a variety of small metazoans (copepods, ostracods, nematodes, etc.).

Plankton composition

During fall sampling, there was a plankton bloom in the harbor. A pair of daytime plankton tows from about 10 cm above the phoronid bed contained approximately 35% dinoflagellates (*Ceratium* sp. and *Gonyaulax* sp.), 12% centric diatoms (two species each of *Chaetoceros* sp. and *Coscinodiscus* sp.), 10% harpacticoid copepods, 7% *Cancer* crab zoea, 6% ostracods (? *Cylindroberis* sp.), and 4% hydromedusae (*Polyorchis* sp.). The remaining living material consisted mostly of pennate diatoms (1.9%) and small flagellates (1.3%).

The tow also contained two types of organic detritus that constituted about 18.8% of the samples; amorphous strings and balls of organic matter and *Zostera marina* fragments averaged 11 and 7% of the samples, respectively.

TABLE III

Particle type abundance of seston* sampled near the tubes of *Phoronopsis viridis*, as mean percentages.

Particle type	\bar{x}
Mineral 100–200 μm encrusted	7.0
Mineral 100–200 μm not encrusted	6.6
Mineral $< 100\ \mu\text{m}$ encrusted	35.0
Floc aggregates	21.1
Plant detritus	3.1
Pollen grains	1.0
<i>P. viridis</i> fecal fragments	13.4
Other fecal matter	7.1
Living diatoms	3.5
Small metazoans	2.1

* Seston is defined as inorganic detritus and organic (living and nonliving) particles. Mean percent abundance was determined by counting and averaging 200 particles at each of eight sampling stations.

TABLE IV

Electivity coefficients of seven most abundant particle types in the stomach of Phoronopsis viridis (data averaged for 20 animals).

Particle type	Electivity
Mineral 100–200 μm (encrusted)	–0.18
Mineral 100–200 μm (not encrusted)	–0.15
Mineral <100 μm (encrusted)	+0.11
Floc aggregates	+0.08
Dinoflagellates	+0.05
<i>P. viridis</i> feces	+0.03
Diatoms	–0.20

Stomach contents

Only six items were routinely present in the stomach of *Phoronopsis*. Positive electivity values suggest a preference for small (< 100 μm) encrusted mineral grains (Table IV). Within this category, 35–75 μm mineral grains were thickly encrusted with loosely adhering organic matter. The electivity data also indicate a preference for floc aggregates along with planktonic dinoflagellates. In 60% of the animals examined, floc aggregates of silt- and clay-sized materials occupied over one-third the volume of the stomach. Small dinoflagellates were selected most often.

A strong avoidance was displayed for mineral grains larger than 100 μm . Organic encrustations, which increase both the sphericity and effective diameter of the particles, further reduced the electivity of large mineral grains. Avoidance of particles in the 100–220 μm range probably is due to either the inability of the frontal cilia on the tentacles to transport the particles or an upper limit to the size of material which can be ingested.

Fecal pellets

The seston and plankton ingested by the animal is defecated at the SWI as easily fragmented fecal pellets. Embedded in the fine-grained mucons matrix were mineral grains (50–90 μm) and an occasional pollen grain or still motile ciliate. The common nudibranch, *Hermisenda crassicornis*, was observed to ingest large numbers of phoronid fecal pellets. The importance of fecal material as a food source for invertebrates has been demonstrated by Newell (1965) and Johannes and Satomi (1966). They have shown that the bacteria which decompose feces are more important nutritionally than the waste material present.

Some of the phoronid fecal material is incorporated into the sediment by numerous small burrowing metazoans which disaggregate and intermix fecal material with the surface sediment. Floc, or organic-mineral aggregates, is probably produced mainly by the mixing of decomposing phoronid (or other) fecal material and sediment. Unmixed fecal material accumulates in surface depressions (ripple troughs, ray feeding pits, etc.), decomposes, and becomes flocculent seston. Resuspension of this material makes it available for ingestion by *Phoronopsis*.

DISCUSSION

In recent years a number of studies have been made of the distribution patterns of benthic species. Most studies suggest that distributions tend toward aggregation and that random or uniform distributions seldom occur in marine (e.g., Clark and Milne, 1955; Angel and Angel, 1967; Warner, 1971) or terrestrial environments (Greig-Smith, 1964; Pielou, 1969). Surprisingly, although a number of soft-sediment species are known to form dense aggregations, particularly brittle stars (Warner, 1971; Broom, 1975; Wilson, Holme, and Barrett, 1977), there is little statistical information on the distribution of individuals within such aggregations.

The present study provides detailed statistical information on *Phoronopsis*, which forms dense aggregations in the intertidal region. Detailed sampling has shown that the population exhibits a clumped distribution whose degree of aggregation remains relatively constant with changes in intertidal elevation and population density. This close association between nearest neighbors produces a pattern of tight clusters.

These results differ from those reported by Johnson (1959) who has used another N-N measure (Clark and Evans, 1955) to examine the spatial pattern of *Phoronopsis*. His results indicate that individual animals tend to be distributed evenly within clusters. Further, he suggests that this pattern of dispersion reflects the minimum distance between individuals necessary for feeding, but he reports no N-N distances nor does he mention a stratification of feeding appendages.

In general, invertebrates that commonly form large, dense aggregations are animals that spend much of their time suspension feeding (e.g., *Ophiothrix fragilis*, Warner, 1971; *Dendraster excentris*, Timko, 1975; *Spisula solida*, Ford, 1925; *Ampelisca* spp., Mills, 1967). This emphasis on feeding activity means that they are continually placed in situations that expose them to disturbance and probably make them highly susceptible to predators. Although a close association between phoronids creates spacing problems among themselves for expansion of the lophophore during feeding, clustering may be an adaptation to predation: when N-N distances are small and lophophores stratified, a close association between individuals can limit the number of animals available to the predatory nudibranch *Hermisenda crassicornis*. I have observed that the sudden retraction of a lophophore creates a disturbance that is transmitted to neighboring animals either by collision of overlapping lophophores or by the generation of sudden perceptible pressure waves that can produce multiple retraction of lophophores. Although the clusters are noncolonial aggregations, this imperfect wave of withdrawal that spreads over part of the cluster produces a response that makes the cluster less vulnerable to predation. Without the response, escape of *Phoronopsis* would depend upon contact with a crawling predator such as *Hermisenda*, which could more easily forage through the cluster.

A dense assemblage of *Phoronopsis* can also stabilize sediment and limit burrowing of large errant infauna which are potentially destructive to the phoronids. In areas of natural contact between the thalassinid sandshrimp *Callinassa californiensis* and *Phoronopsis*, the burrowing activity of the shrimp can act to set the upper limit of *Phoronopsis* intertidal range (Ronan, 1975). This type of

interaction in which one population is limited while the other is not has been termed "amensalism" (Odum, 1971). While there is no evidence of shrimp predation at low population densities of *Phoronopsis*, manipulated tubes are frequently found at unnatural depths, and occasionally tubes are found to be actually broken with pieces of tube offset and/or rotated on opposite sides of *Callianassa* burrows. Former occupants of broken and disoriented tubes were found to be living free in the sediment in the process of building new tubes in contact with the water column. This nonpredatory but potentially destructive interaction with *Callianassa* constitutes a form of "substrate amensalism" that operates at low tube densities to restrict the intertidal distribution of *Phoronopsis*. However, when *Phoronopsis* densities are high and N-N distances small, the numerous tubes buttress the sediment and constitute a subsurface obstruction to some large burrowing organisms. Dense clusters of *Phoronopsis* are only rarely undermined by foraging *Callianassa* (Ronan, in preparation).

Cluster formation may, therefore, permit *Phoronopsis* to coexist in sandflats with an established errant infauna which it might not otherwise successfully inhabit. However, cluster formation also could have other advantages: first, the proximity of large numbers of adults could insure gamete fertilization during the breeding season; and secondly, clustering may have even more subtle, advantageous effects on feeding. The feeding currents of an individual may work better with other individuals nearby. Aggregated feeding currents may possibly modify localized water flow with the clusters acting as "food funnels" for the accumulation of both resuspended and planktonic food material. The thick seston layer which develops within phoronid clusters, but not in the open spaces between clusters, may be a manifestation of the funneling effect.

Previous reports of diet composition and selectivity in the Phoronida are lacking. However, there are studies which are pertinent to the present work. Whitlatch (1974 and personal communication) has shown that the polychaete *Pectinaria gouldii* concentrates organic material found in the sediment by preferentially ingesting large encrusted mineral grains, fecal material, and floc aggregates. He suggests that there are probably several major sources of the organic material that encrusts mineral grains and forms low-density floc aggregates (terrigenous input, plant debris, decomposing fecal material, and metabolites of plankton and bacteria) and food value differences may depend upon the original source, state of decay, and number of times the material has passed through an animal gut. Further, he has demonstrated that the feeding of *Pectinaria* channels large amounts of organic material to the SWI where it can become available to other organisms. At the depositional interface, the combined effects of bioturbation and tidal energy create a constant upwelling and recycling of organic material from the sediment into the water column (Rhoads, 1973). The data on size selectivity and diet presented in the present report show that resuspended encrusted mineral grains, fecal pellets and floc materials, and plankton are of trophic significance to a suspension-feeding phoronid. The continuous feeding and stable generalized diet are undoubtedly important factors which have allowed *Phoronopsis* to attain great abundance in shallow water coastal embayments.

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SUMMARY

1. In the intertidal zone of Bodega Harbor, California, the phoronid, *Phoronopsis viridis*, aggregates in clusters often composed of thousands of tightly aggregated individuals (up to 150,000/m²). Within a dense cluster, there is a spacing problem for expansion of the lophophores. When nearest-neighbor distances are small, a stratification of feeding appendages is a workable solution to the spacing problem, allowing simultaneous expansion of clustered feeding appendages.

2. Suspension-feeding specimens of *Phoronopsis* expand their lophophores and collect food items from the turbid near-bottom layers of water. Comparison of ingested items with material collected where the phoronids feed indicates a preference for small (< 100 μ m) organic encrusted mineral grains, floc aggregates, and fecal material, all resuspended from the depositional interface. Also taken to a lesser extent are plankton bloom species, such as diatoms and dinoflagellates.

3. The fact that *Phoronopsis* forms dense assemblages in the intertidal zone has consequences when the community structure of sandflat areas is considered. Although it is probable that no single factor can explain aggregation in *Phoronopsis*, two possible factors, constituting strong selection pressures for cluster formation, are relative immunity from disturbance by large burrowing infauna and protection from predation by crawling predators.

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